MADROÑO, Vol. 59, No. 4, pp. 223–229, 2012

DUDLEYA CRASSIFOLIA (CRASSULACEAE), A NEW SPECIES FROM NORTHERN BAJA CALIFORNIA, MEXICO

MARK W. DODERO[1] AND MICHAEL G. SIMPSON
Department of Biology, San Diego State University, San Diego, CA 92182
mdodero@reconenvironmental.com

ABSTRACT

Dudleya crassifolia is described as new. It belongs to a complex of taxa within subgenus *Hasseanthus* that have a white (occasionally pale yellow) corolla with a conspicuous, "musky-sweet" odor. It differs from related species of this complex in having a thicker petiole, a leaf blade that is only slightly wider than the petiole, and conspicuous dried leaf bases persisting on the caudex. This species is very rare, currently known only from a single population of scattered individuals (total area of coverage less than one hectare), on sandstone bluffs at Colonet Mesa of north coastal Baja California, Mexico.

Key Words: Baja California, Crassulaceae, *Dudleya*, *Dudleya crassifolia*, *Hasseanthus*, maritime chaparral, Mexico.

The genus *Dudleya* Britton & Rose (1903), consists of approximately 33 species and 54 taxa (including infraspecies) of leaf-succulent perennials, native to California, Oregon, Arizona, Nevada, and Utah, USA, and to Baja California, Baja California Sur, and Sonora, Mexico (Wiggins 1980; Kartesz 2011; McCabe 2012). Species of *Dudleya* differ from those of related genera, such as *Sedum*, in having axillary inflorescences (Moran 1942).

Dudleya subgenus *Hasseanthus*, as traditionally treated (Moran 1950, 1951; Munz 1974; Bartel 1993; McCabe 2012) contains five species and six taxa: *D. bloclmaniae* (Eastw.) Moran subsp. *bloclmaniae, D. blochmaniae* (Eastw.) Moran subsp. *insularis* (Moran) Moran, *D. brevifolia* (Moran) Moran, *D. multicaulis* (Rose) Moran, *D. nesiotica* (Moran) Moran, and *D. variegata* (S. Watson) Moran. Species in subgenus *Hasseanthus* are characterized by their drought-deciduous leaf duration and hypogeous caudex, and range from San Luis Obispo Co., California to northern Baja California, Mexico. While attempting to relocate Baja California populations of *D. blochmaniae* previously collected by the late Dr. Reid Moran, the first author discovered a distinct form of *Dudleya* at Colonet Mesa of north, coastal Baja California. We believe this form of *Dudleya* should be treated as a new species using a taxonomic (morphologic) species concept (Cronquist 1978, 1988), in which species are circumscribed based on the discontinuity of morphological features.

TAXONOMY

Dudleya crassifolia Dodero & M. G. Simpson, sp. nov. (Figs. 1, 2).—Type: MEXICO, Baja California, ca. 7 miles southwest of Colonet, reddish sandstone bluffs on mesa, maritime chaparral, associates: *Adenostoma fasciculatum, Agave shawii, Artemisia californica, Ceanothus verrucosus, Cneoridium dumosum, Dudleya attenuata* subsp. *a.*, *Dudleya* cf. *ingens*, *Ephedra* sp., *Eriogonum fasciculatum, Ferocactus viridescens, Helianthemum scoparium, Rhus integrifolia, Salvia brandegeei, Stephanomeria* sp., clay sub-soil, with upper layer of sand and surface iron concretions, 95 meters elevation, 31.00°N, 116.30°W, 3 June 1991, *M. Dodero s.n.* (holotype: SD; isotypes: BCMEX, RSA, UC).

Diagnosis: *Dudleya crassifolia* is similar to *D. bloclmaniae* subsp. *bloclmaniae*, *D. bloclmaniae* subsp. *insularis*, *D. brevifolia*, and *D. nesiotica*, but differs in having a thicker (2–3.3 mm) petiole, a leaf blade width at maturity only slightly greater than the petiole width (blade width:petiole width ratio 1.2–1.4), and conspicuously persistent dried leaf bases on the subterranean caudex.

Description: **Plants** single to branched at base with up to 10 rosettes. **Caudex** cylindrical to irregular 1.0–5.5 cm long, 2–20 mm thick, with conspicuous, dried leaf bases persisting from multiple, previous seasons. **Leaves** in a rosette, 3–21, oblanceolate in mature plants to globose in juveniles, apex acuminate to acute to rounded (especially in juvenile plants), often mucronulate, 6–35 mm long, 3–11 mm wide, 1.5–7.5 mm thick, the petioles 0.9–12.4 mm long, 1.0–8.0 mm wide, 2–3.3 mm thick, the base truncate, 1–12 mm wide (narrower petioles are found in juvenile plants), leaves drought deciduous, bases persistent. **Inflorescence** 6–17 cm tall, ascending to inclined, 1.5–

[1] Present address: RECON Environmental, Inc., 1927 5th Ave, San Diego, CA 92101.

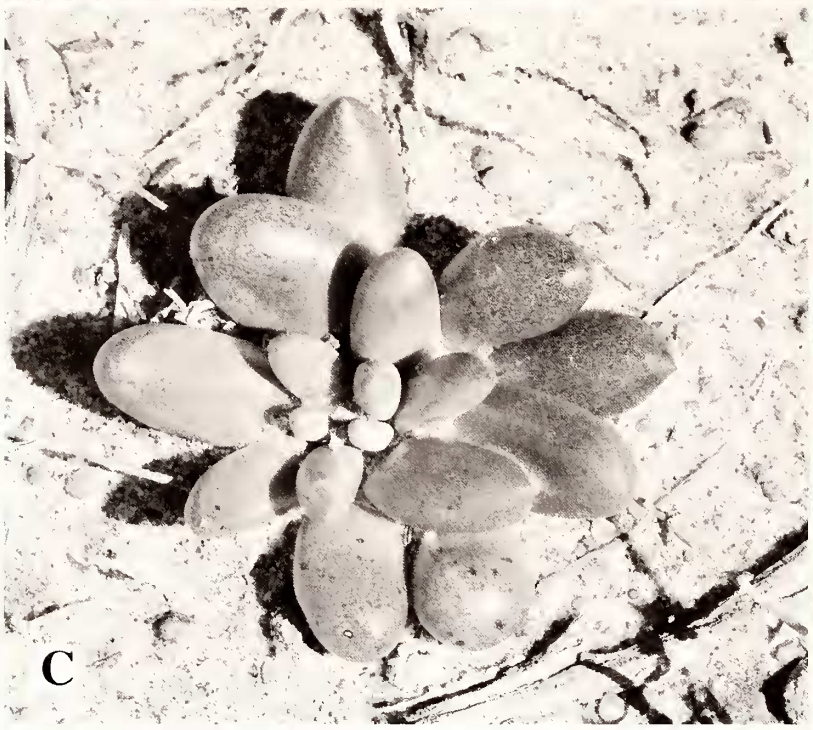

FIG. 1. Habit shots, Colonet Mesa, Baja California, Mexico. A. Open, flat area of iron concretions, surrounded by mixed maritime chaparral. B–D. *Dudleya crassifolia*. B–C. Plants prior to flowering, showing one or more rosettes of thick, succulent leaves. D. Flower and buds of inflorescence. Note divergent, white corolla lobes.

3.5 mm thick at the base, bracts within 1–2 cm of the base. Lower bracts 7–19, ovate to widely ovate, acute, the lowermost 9–20 mm long, 6–11 mm wide, 3–7 mm thick. Inflorescence axis usually with 2–3 ascending branches that rebranch 0–1 times, the ultimate cincinni 1–4 cm long, each with 2–10 flowers. **Pedicels** ascending, 1–3.5 mm long. **Flowers** with a characteristic musky odor. Calyx 3.5–6.5 mm wide, 3.5–6 mm long, lobes narrowly triangular to ovate, apex acute to acuminate, 2.5–4 mm long, 1.5–2.5 mm wide. Corolla 4–5 mm wide at the base, 14–17 mm wide at apex, basally connate 1–2 mm, lobes white, keel and base maroon, often suffused with maroon throughout, elliptic, 8–12 mm long, 3–4.5 mm wide, ascending to divergent, apex acute. **Stamen** filaments 6–8 mm long, epipetalous, adnate 1–2 mm; anthers 1 mm long, 0.8 mm wide, red before dehiscence, yellow afterward. Nectar glands light yellow, 1.2 mm wide. **Gynoecium** 5–8 mm long, pistils erect to ascending at anthesis, ovaries five, 4–6 mm long, styles 1–2 mm long. Fruits not described. **Chromosome number**: $n = 34$ (Dodero 1995).

Distribution and Habitat: *Dudleya crassifolia* is endemic to the southern end of Colonet Mesa, southwest of Colonet, Baja California, Mexico (Fig. 3), in maritime chaparral, on reddish sandstone bluffs with a subsoil of clay covered with sand and iron concretions. Its total area of occurrence is less than one hectare. (See Discussion.)

Phenology: *Dudleya crassifolia* flowers from late May to June.

Etymology: The specific eptithet, *crassifolia*, is from the Latin *crassus* "thick" and *folius* "leaf," in reference to the thick, succulent leaves.

Suggested common name: Thick Leaf Dudleya.

Paratypes: MEXICO, Baja California, ca. 7 mi SW of Colonet, reddish sandstone bluffs on

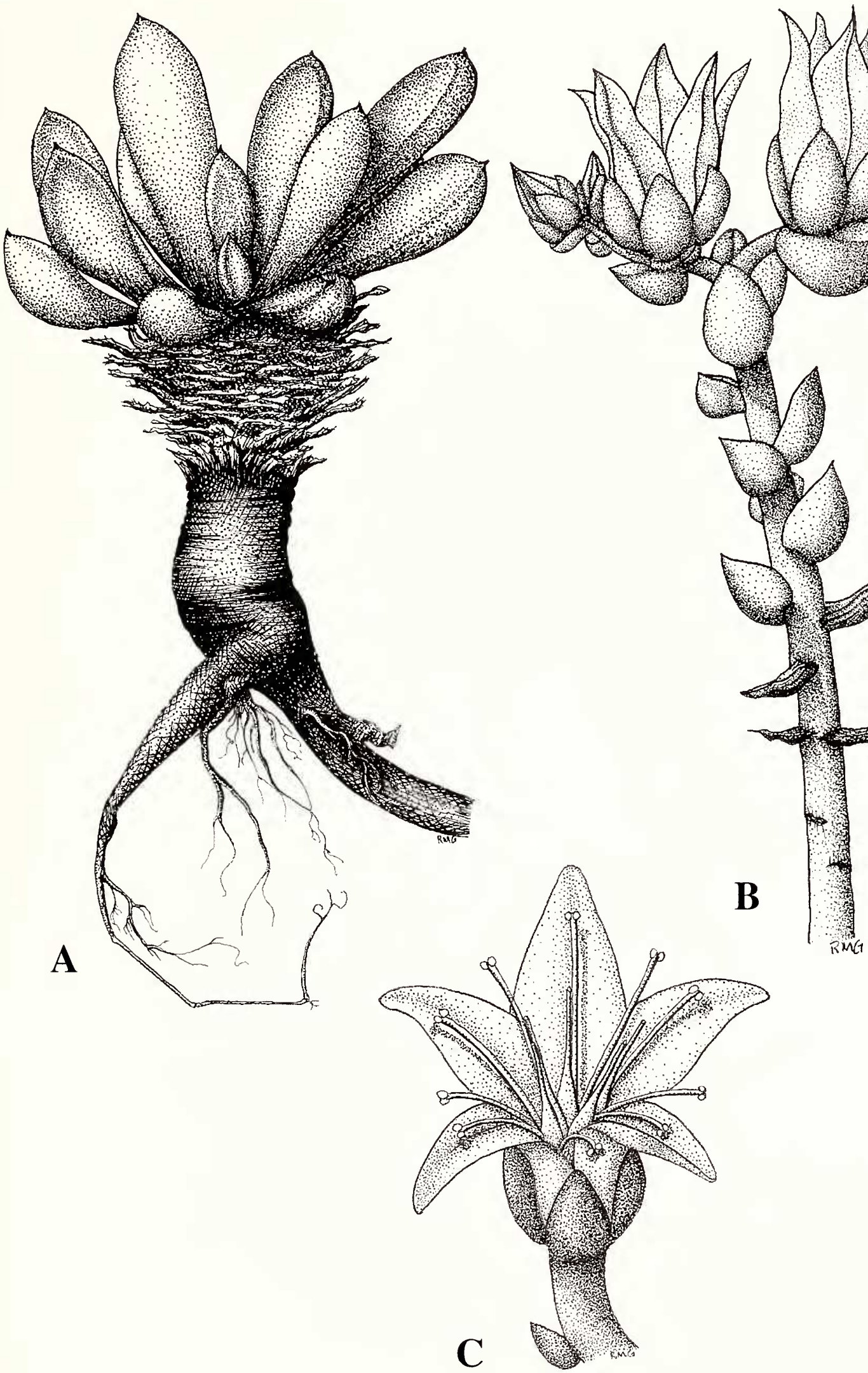

FIG. 2. Line drawings of *Dudleya crassifolia* from type population. A. Caudex, showing roots and apical rosette of leaves at apex. Note remains of old leaf bases below rosette. B. Inflorescence. Note succulent bracts along primary axis. C. Open flower. Note recurved corolla lobes, the upper half divergent.

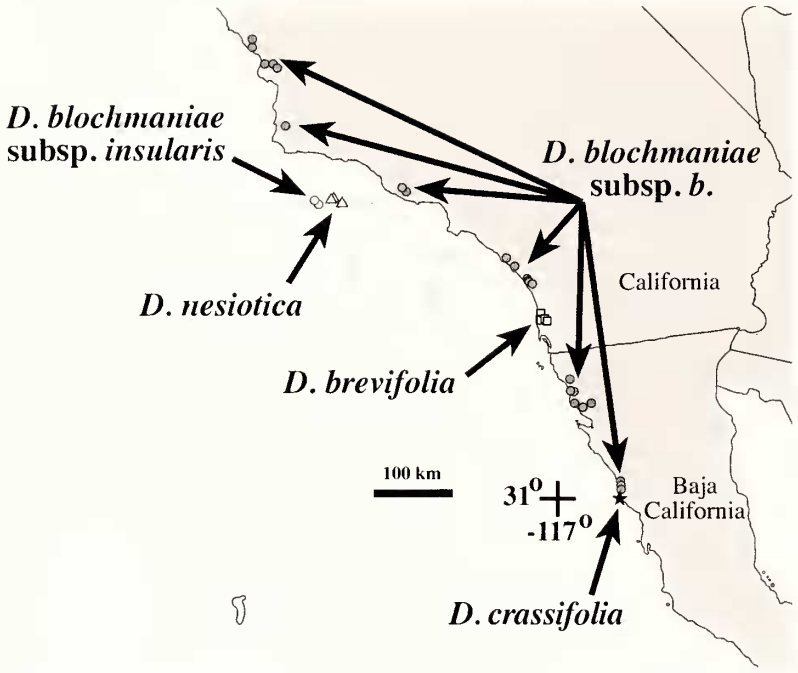

FIG. 3. Distribution map, from geo-referenced herbarium collections, of the taxa of the "*blochmaniae*" complex of *Dudleya*, subgenus *Hasseanthus*. Note wide distribution of *D. blochmaniae* subsp. *blochmaniae* (gray circles) and restricted distributions of *D. blochmaniae* subsp. *insularis* (white circles), *D. brevifolia* (white squares), *D. nesiotica* (white triangles), and the single known population of *D. crassifolia* (black star).

mesa, maritime chaparral, associates: *Adenostoma fasciculatum, Agave shawii* var. *shawii, Artemisia californica, Ceanothus verrucosus, Cneoridium dumosum, Dudleya attenuata* subsp. *a.*, *Dudleya* cf. *ingens*, *Ephedra* sp., *Eriogonum fasciculatum, Ferocactus viridescens, Helianthemum scoparium, Rhus integrifolia, Salvia brandegeei, Stephanomeria* sp., clay sub-soil, with upper layer of sand and surface iron concretions, 95 m elev., 31.00°N, 116.30°W, 1 June 1992, *M. Dodero s.n.* (SBBG, SDSU, MEXU, UCR); towards the point of Punta Colonet, on the mesa, small sandstone outcrop, in maritime chaparral, associates: *Adenostoma fasciculatum, Gambelia juncea* [*Galvezia j.*], *Cneoridium dumosum, Ceanothus verrucosus, Artemisia californica, Ferocactus viridescens, Agave shawii, Salvia brandegeei,* and *Antirrhinum nuttallianum*, ca. 84 m elev., 31.00°N, 116.31°W, 21 June 2008, *Vanderplank C-66* (RSA, SD).

DISCUSSION

Morphological Distinctiveness

Dudleya crassifolia is a distinctive entity of the genus that we feel warrants status as a separate species. It is a member of a group of species within subgenus *Hasseanthus*, this group also including *D. blochmaniae* subsp. *blochmaniae*, *D. blochmaniae* subsp. *insularis*, *D. brevifolia*, and *D. nesiotica*. These taxa, referred to here as the "*blochmaniae* complex," share a white (rarely pale yellow in *D. brevifolia and D. nesiotica*) corolla color and presence of a musky or "musky sweet" (McCabe 2012) flower odor, a combination that appears to be unique in the genus. All members of subgenus *Hasseanthus* are similar in juvenile leaf characteristics (Dodero 1995). In mature, adult leaves *Dudleya crassifolia* overlaps with members of the *blochmaniae* complex in blade width and petiole width, but in *D. crassifolia* the leaf blade is only slightly wider than the petiole (blade width:petiole width ratio 1.2–1.4), while in the other members of the complex the blade is two to more than four times as wide as the petiole (blade width:petiole width ratio 2.1–4.7) (Dodero 1995). *Dudleya crassifolia* also differs from the other four members of the *blochmaniae* complex in having significantly thicker petioles (2–3.3 mm in *D. crassifolia*; ranging 0.4–1.7 mm in the other four taxa; Dodero 1995).

The other two members of subgenus *Hasseanthus*, *Dudleya multicaulis* and *D. variegata*, differ from *D. crassifolia* and the rest of the *blochmaniae* complex in having consistently yellow petals that lack the characteristic flower odor. *Dudleya crassifolia* also differs from *D. multicaulis* in its thicker, oblanceolate leaves with a smaller blade length to width ratio (2–3); in contrast, *D. multicaulis* has linear, more terete leaves with a much greater blade length to width ratio (6–11) (Dodero 1995). *Dudleya crassifolia* differs from *D. variegata* in the former's greater petiole width and leaf thickness and smaller leaf-blade width to petiole width (1.2–1.4 in *D. crassifolia* versus ratio 2.6–4.1 in *D. variegata*). Finally, *Dudleya crassifolia* differs from all other species of subgenus *Hasseanthus* in having conspicuous, persistent dried leaves at the caudex base. We have to date seen no evidence for hybridization between *D. crassifolia* and other *Dudleya* species.

According to a phylogenetic study using allozyme data (Dodero 1995), *Dudleya crassifolia* is most closely related to the *D. blochmaniae* subsp. *blochmaniae* populations that are found within a few miles of *D. crassifolia* (Fig. 3). These *D. blochmaniae* populations occupy patches of clay soils along with associates such as *Chlorogalum parviflorum* and *Deinandra* spp. Interestingly, the *Dudleya blochmaniae* populations in this general area of Baja California are known to be tetraploid ($n = 34$) or hexaploid ($n = 51$) (Uhl and Moran 1953), the former identical to *D. crassifolia* ($n = 34$; Dodero 1995). In contrast, populations of *D. blochmaniae* in California are all diploid ($n = 17$) (Uhl and Moran 1953).

Distribution, Evolution, Associates, and Geology

Dudleya crassifolia is found approximately seven miles southwest of Colonet, Baja California. It is apparently restricted to a few small, reddish sandstone bluffs of Colonet Mesa,

defined as the area "south of the road to San Antonio del Mar" (Harper et al. 2011). This population consists of scattered individuals occupying an area estimated at less than one hectare. The bluffs where this species is found are covered with iron concretions. Just east of the sandy bluff is a partially stabilized dune formation with typical dune scrub (Holland and Keil 1995).

An approximate distribution map of the taxa of the *blochmaniae* complex, assembled from georeferenced data (BajaFlora 2012; CCH 2012; SEINet 2012) is seen in Fig. 3. *Dudleya blochmaniae* subsp. *blochmaniae* has a wide distribution, from coastal San Luis Obispo Co., California to coastal northern Baja California. The other taxa of *Dudleya* in this complex have a narrow distribution, *D. blochmaniae* subsp. *insularis* restricted to Santa Rosa Island (Santa Barbara Co.), *D. brevifolia* restricted to southwestern San Diego Co., *D. nesiotica* restricted to Santa Cruz Island (Santa Barbara Co,), and *D. crassifolia* restricted to Colonet Mesa of coastal northern Baja California (Fig. 3). A working hypothesis is that *D. blochmaniae* subsp. *b.* may represent a widespread, possibly paraphyletic species (after Olmstead 1995), from which the other taxa of the *blochmaniae* complex have diverged from isolated populations. This notion remains to be tested with molecular phylogenetic studies.

Plant associates growing in the immediate vicinity of *D. crassifolia* include *Adenostoma fasciculatum* Hook & Arn., *Agave shawii* Engelm., *Artemisia californica* Less., *Ceanothus verrucosus* Nutt., *Cneoridium dumosum* (Torr. & A. Gray) Baill., *Dudleya attenuata* (S. Watson) Moran subsp. *attenuata*, *Dudleya* cf. *ingens*, *Ephedra* sp., *Eriogonum fasciculatum* Benth., *Ferocactus viridescens* (Torr. & A. Gray) Britton & Rose, *Helianthemum scoparium* Nutt., *Rhus integrifolia* (Nutt.) W.H. Brewer & S. Watson, *Salvia brandegeei* Munz, and *Stephanomeria* sp. This community is best categorized as maritime chaparral, with surrounding areas supporting Martirian succulent scrub, a more xerophytic vegetation type (Westman 1983). *Dudleya crassifolia* occurs in openings of this maritime chaparral.

The associated plant species and red sandstone bluffs are apparently part of an ancient beach ridge formation similar to the sandstone bluffs found near Del Mar, San Diego Co., California, where *D. brevifolia* is found. *Dudleya brevifolia* occurs on bluff tops of the Linda Vista Formation, which were formed as the sea receded during the Pleistocene. The surface of these bluffs is covered with small iron concretions similar to the one at Colonet Mesa.

Herbivory, Pollination, and Seed Dispersal

Observations indicate that herbivory, presumably by rabbits (rabbit scat is frequently seen on the bluff) and small rodents, appears to be significant. In November 1992, before any rain had fallen and conditions were very dry, many dormant plants had been excavated by animals and eaten. The leaves of actively growing plants were eaten by animals during the winter growing season. In cultivation, plants in which the top of the tuberous caudices were exposed above the soil surface, and which appeared to be dead, are capable of re-sprouting from beneath the soil surface, often forming multiple rosettes.

Potential pollinators were observed and captured. Two species of wasp, *Stenolia duplicata* and *Bembix occidentalis,* both members of the sand wasp group (family Crabronidae, subfamily Bembicinae), were seen visiting flowers. Typically these wasps feed on flies, but they will supplement their diet with pollen (Borror and White 1970; Borror et al. 1989). Another potential pollinator, the soft-winged flower beetle, *Dasytes* sp. (family Melyridae, subfamily Dasytinae) lives in the flowers. These beetles are usually found at the base of the carpels near the nectar glands.

Seed dispersal appears to be accomplished mostly by wind and water movement. Seeds sprinkled on the soil surface during a 15–20 knot wind were observed to move along with grains of sand. If moisture and temperature conditions are optimal, germination of *D. crassifolia* seeds is rapid, often occurring in less than 72 hours. Recruitment of seedlings appears to be highest in areas of moderate soil deposition and underneath shrubs where seeds are transported by the wind (Dodero, personal observations).

Conservation

The Colonet region is estimated to have the highest plant diversity in Baja California (Harper et al. 2011). The region has 435 documented vascular plant taxa, of which 383 are native to Baja California, and 52 are endemic or nearly endemic to the state or peninsula (Harper et al. 2011). Eighteen of these taxa are listed by the California Native Plant Society as 1B, "rare, threatened, or endangered in California and elsewhere" (CNPS 2012). Three of these taxa are on the Mexican NOM 059 list of protected taxa; five of these taxa are narrow endemics, known only from the Colonet region (Harper et al. 2011).

Of the five taxa that are local endemics to the Colonet region, *Dudleya crassifolia* is perhaps the rarest and most geographically restricted, being found at a single locality on sandstone bluffs at Colonet Mesa. Its rarity and limited distribution warrant focused protective measures. Unfortunately, Colonet Mesa and the surrounding region is threatened by a pending proposal from the Mexican government to construct a seaport

(which would be accompanied by massive infrastructure and a large, projected growth in human population) just below the southern tip of the mesa at Punta Colonet. This project could seriously impact this unique and diverse region without major conservation efforts to protect sensitive habitat (Clark et al. 2008; Harper et al. 2011).

Taxonomic Key

A revised key to species of subgenus *Hasseanthus*, modifed from McCabe (2012), is presented below.

1. St gen below surface, not elongate, gen simple, unbranched; leaves deciduous, vernal, generally petioled (barely in *D. crassifolia*) (subg. *Hasseanthus*)
   2. Flower odor absent; corolla consistently yellow
      3. Leaves 4–15 cm long, linear, ± narrowed above base, tip sharply acute; petals basally connate 1–2 mm . . . . . *D. multicaulis*
      3′ Leaves 1–7 cm long, oblanceolate to spoon-shaped, strongly narrowed above base (to gen 0.5–3 mm wide), tip acute to obtuse; petals basally connate 0.5–1 mm . . . . . *D. variegata*
   2′ Flower odor musky-sweet; corolla white to white-maroon (rarcly pale yellow in *D. brevifolia* and *D. nesiotica*)
      4. Leaf blade only slightly wider than petiole (ratio 1.2–1.4), petioles 2–3.3 mm thick; caudex with conspicuous, dried leaf bases persisting from multiple, previous seasons . . . . . *D. crassifolia*
      4′ Leaf blade two to more than four times as wide as the petiole (ratio 2.1–4.7), petiole 0.4–1.7 mm thick; caudex lacking conspicuous, dried leaf bases from previous seasons
         5. Petals ascending, 7–14 mm, 3.5–5.5 mm wide, fused 1–2 mm; fr ascending; lf base 3–12 mm wide . . . . . *D. nesiotica*
         5′ Petals spreading, 5–10 mm, 2–4 mm wide, fused gen <1 mm; fr spreading; lf base 1–4 mm wide
            6. Lower bracts <1.5× longer than wide; lvs 7–15 mm, ± spheric to spoon-shaped; petiole narrow . . . . . *D. brevifolia*
            6′ Lower bracts >2× longer than wide; lvs 10– 60 mm, ± oblanceolate to club-shaped; petiole ± narrow . . . . . *D. blochmaniae*
               7. Lvs gen <12, not to ± glaucous . . . . . subsp. *blochmaniae*
               7′ Lvs gen >15, glaucous or ± so . . . . . subsp. *insularis*

1′ St gen above surface, often elongate, often branched; lvs gen evergreen, ± not petioled (remaining *Dudleya* species)

Acknowledgments

We thank Jim Berrian and Robyn Garcia for providing transportation and assisting in field work, Bruce and Karen April for help in the field, Robyn Garcia for providing the illustrations, and Kim Marsden for assistance in field work and moral support. Dave Truesdale was indispensable in the allozyme work cited here. Finally, we thank three anonymous reviewers for valuable comments made in review of the manuscript.

Literature Cited

BajaFlora. 2012. The flora of Baja California. Specimen data obtained from a combined multi-herbarium specimen database called the Baja California Botanical Consortium hosted by the San Diego Natural History Museum. San Diego, CA.Website: http://www.bajaflora.org [accessed 18 April 2012].

Bartel, J. A. 1993. *Dudleya*. Pp. 525–530 *in* J. C. Hickman (ed.), The Jepson manual: higher plants of California. University of California Press, Berkeley, CA.

Borror, D. J. and R. E. White. 1970. A field guide to the insects of America north of Mexico. Houghton Mifflin, Boston, MA.

———, C. A. Triplehorn, and N. F. Johnson. 1989. An introduction to the study of insects, 6th ed. Saunders College Publishing, Philadelphia, PA.

Britton, N. L. and J. N. Rose. 1903. New or noteworthy North American Crassulaceae: *Dudleya* Britton & Rose, gen. nov. Bulletin of the New York Botanical Garden 3:12–28.

Consortium of California Herbaria (CCH). 2012. Website: http://ucjeps.berkeley.edu/consortium [accessed 18 April 2012].

Clark, K. B., M. Dodero, A. Chavez, and J. Snapp-Cook. 2008. The threatened biological riches of Baja California's Colonet Mesa. Fremontia 36:3–10.

California Native Plant Society (CNPS). 2012. Inventory of rare and endangered plants (online edition, v8-01a). California Native Plant Society, Sacramento, CA. Website: http://www.rareplants.cnps.org/ [accessed 23 February 2012].

Cronquist, A. 1978. Once again, what is a species? Pp. 3–20 *in* J. A. Ramberger (ed.), Biosystematics in agriculture. Allanheld & Osmun, Montclair, NJ.

———. 1988. The evolution and classification of flowering plants, 2nd ed. New York Botanic Garden, New York, NY.

Dodero, M. W. 1995. Phylogenetic analysis of *Dudleya* subgenus *Hasseanthus* (Crassulaceae) using morphological and allozyme data. M.S. thesis, San Diego State University, San Diego, CA.

Harper, A. B., S. Vanderplank, M. Dodero, S. Mata, and J. Ochoa. 2011. Plants of the Colonet region, Baja California, Mexico, and a vegetation map of Colonet Mesa. Aliso 29:25–42.

Holland, V. L. and D. J. Keil. 1995. California vegetation. Kendall/Hunt, Dubuque, IA.

Kartesz, J. T. 2011. The biota of North America program (BONAP). North American Plant Atlas. Chapel Hill, NC. Website http://www.bonap.org/). [maps generated from Kartesz, J. T. 2010. Floristic Synthesis of North America, Version 1.0. Biota of North America Program (BONAP)], [accessed 01 December 2011].

McCabe, S. W. 2012. *Dudleya*. Pp. 666–673 *in* B. G. Baldwin, D. H. Goldman, D. J. Keil, R. Patterson, T. J. Rosatti, and D. H. Wilken, (eds.), The Jepson manual: vascular plants of California, 2nd ed. University of California Press, Berkeley, CA.

Moran, R. 1942. The status of *Dudleya* and *Stylophyllum*. Desert Plant Life 14:149–157.

———. 1950. Notes on *Hasseanthus* I. Desert Plant Life 22:6–82.

———. 1951. Notes on *Hasseanthus* II. Desert Plant Life 22:101–105.

Munz, P. A. 1974. A flora of Southern California. University of California Press, Berkeley, CA.

Olmstead, R. G. 1995. Species concepts and plesiomorphic species. Systematic Botany 20:623–630.

Southwest Environmental Information Network (SEINet). 2012. Website: http://swbiodiversity.org/seinet/index.php [accessed 18 April 2012].

Uhl, C. H. and R. Moran. 1953. The cytotaxonomy of *Dudleya* and *Hasseanthus*. American Journal of Botany 40:492–502.

Westman, W. E. 1983. Xeric Mediterranean-type shrubland associations of Alta and Baja California and the community/continuum debate. Vegetatio 52:3–19.

Wiggins, I. L. 1980. Flora of Baja California. Stanford University Press, Stanford, CA.